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High resource capture and use efficiency and prolonged growth season contribute to invasiveness of *Eupatorium adenophorum*

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Abstract To explore the traits contributing to invasion success of *Eupatorium adenophorum*, a noxious invasive perennial forb throughout the subtropics in Asia, Oceania, Africa, and USA, we compared the differences in ecophysiology and phenology between the invader and native *E. japonicum* under eight treatment combinations of two irradiances and four nitrogen additions in a two-year shadehouse experiment. The invader had significantly higher mass-based light-saturated photosynthetic rate (P_{max}) than its native congener in all treatments, contributing to higher photosynthetic nitrogen-, phosphorus-, and energy-use efficiencies. The higher P_{max} of the invader was associated with its higher nitrogen concentrations in the photosynthetic apparatus, which resulted from higher leaf nitrogen allocation to photosynthesis. The invader had higher specific leaf area and stomatal conductance at most of the treatments, also contributing to its higher P_{max}. The invader was not constrained by the negative correlation between leaf lifespan and specific leaf area or P_{max}. Leaf lifespan and total leaf area of the invader were greater than those of the native. From November to March the native congener was leafless, whereas the invader maintained a large area of leaves with relatively high P_{max}. Biomass accumulated in these months accounted for more than 40 % of the total biomass of the invader. Our results indicate that both the ability to capture and utilize resources efficiently and the ability to use resources when they are unavailable to natives contribute to invasion success

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of *E. adenophorum* and emphasize the importance of exploring multiple, non-mutually exclusive mechanisms for invasions.

Keywords Benefit–cost analysis · Construction cost · Nitrogen allocation · Photosynthetic energy-use efficiency · Leaf phenology · Specific leaf area

Introduction

Many plant species have been intentionally or accidentally introduced outside their original habitats by humans. A small proportion of them have become invasive, changing species composition, structure, and function of invaded ecosystems and posing great economic and biological threats worldwide (Pimentel et al. 2001; Xu et al. 2006). Understanding the mechanisms underlying biological invasions is a necessary first step to predict and control the spread of invasive species (Pyšek and Richardson 2007).

Growth rate is a vital trait for plants because both survival and reproduction rely on it. High growth rate, which is associated with high photosynthetic rate, has been found to contribute to invasiveness of some alien plants (Zheng et al. 2009; Dawson et al. 2011; Lamarque et al. 2011). Thus, comparisons of photosynthesis and related traits between invasive and non-invasive plant species may help understand fundamental aspects of plant invasions (Baruch and Goldstein 1999; Feng et al. 2009). For example, increasing leaf nitrogen (N) concentration (N_L) and/or N allocation to photosynthesis may promote invasiveness of alien plants by increasing photosynthetic capacity (Feng et al. 2007; Mozdzer and Zieman 2010). Increased N allocation to photosynthesis may also lead to increased photosynthetic N- and phosphorus (P)-use efficiencies (PNUE and PPUE), facilitating invasion success of alien plants even in resource-poor environments (Feng et al. 2007, 2009; Funk and Vitousek 2007).

Cell walls are another major N sink (Lambers and Poorter 1992) because they contain many structural and functional proteins. A tradeoff for N allocation to cell walls versus photosynthesis has been documented for some plant species (Onoda et al. 2004; Takashima et al. 2004). Recent studies found that in an apparent response to the lack of natural enemies, invasive *Ageratina adenophora* (Syn. *Eupatorium adenophorum*) has evolved increased N allocation to photosynthesis and decreased allocation to cell walls (defense), contributing to increased photosynthesis (Feng et al. 2009, 2011). Similar results were also found in invasive *Spartina alterniflora* under nitrogen-poor treatment (Qing et al. 2012). However, this tradeoff for N allocation was not found in two recent studies of non-invasive plant species (Harrison et al. 2009; Hikosaka and Shigeno 2009).

Besides photosynthesis (energy input), the efficiency of energy expenditure on biomass production (measured by biomass construction cost; CC) also influences plant growth and reproduction, and therefore invasiveness of introduced plants (Feng et al. 2011). Increased photosynthesis may not lead to increased growth if it is achieved by disproportionately high CC. Comparable or even lower photosynthesis (Daehler 2003) and comparable or even higher CC (Baruch and Goldstein 1999; Feng 2008; Feng et al. 2007; Lei et al. 2012) have also been documented for some invasive species relative to co-occurring natives. Plants may benefit from high photosynthesis per unit leaf CC, i.e. high photosynthetic energy-use efficiency (PEUE). However, little effort has been made to compare the differences in PEUE between invasive and native plants (but see Song et al. 2009; Osunkoya et al. 2010; Lei et al. 2012).

In addition, extending growing periods by early budding and/or late leaf shedding can also increase biomass accumulation and competitive ability. A prolonged growing season has been reported for several invasive species relative to co-occurring natives (Xu et al. 2007; Fridley 2012). Thus, it is important to study the relative role of the ability to capture and use resources efficiently and the ability to use resources when they are unavailable to natives in increasing biomass accumulation of invasive plants.

To elucidate the traits contributing to success of noxious invasive *E. adenophorum*, we compared a suite of traits between this species and its co-occurring native congener *Eupatorium japonicum* for 2 years under eight treatment combinations of two irradiances and four N additions in a shadehouse experiment. Such phylogenetic comparisons can shed more light on biological invasions because of more closely shared traits and resource requirements than unrelated plants (Daehler 2003). It is well known that alien plant invasions are environment-dependent and that increasing resource availability generally facilitates alien

plant invasions (Davis et al. 2000; Daehler 2003). We tested the hypotheses that invasive *E. adenophorum* (1) allocates a higher fraction of leaf N to photosynthesis at the expense of cell walls; (2) has higher light-saturated photosynthetic rate (P_{max}), PNUE, and PPUE; and (3) shows a quicker-return energy-use strategy at leaf level, i.e. a higher PEUE. We also evaluated whether phenological differences between *E. adenophorum* and *E. japonicum* play a role in the invasiveness of *E. adenophorum*.

Materials and methods

Species and treatments

This study was conducted in a shadehouse located in Qujing (25°31′19″ N, 103°44′50″ E, 1,880 m above sea level), Yunnan Province, southwest China. Here, the mean annual temperature is 14.5 °C and the average annual precipitation is 1,200 mm.

Eupatorium adenophorum is native to Mexico and Central America but a noxious invasive plant throughout the rest of the subtropics (Feng et al. 2011). It spread into Yunnan Province, in southwestern China, from Burma and Vietnam in the 1940s. Now it occurs in seven provinces of southwest China. It invades disturbed habitats including roadsides, abandoned fields, and disturbed pastures and forests, replacing native plant species. *Eupatorium japonicum*, native to many provinces in China, occurs in many habitats including understory and edge of forests, shrubs, and grasslands. It can be outcompeted by *E. adenophorum* in fields (personal observation). Both the invasive and native species are 1–2 m tall perennial forbs.

Seeds of the two species were collected in a secondary forest (25°05′449″N, 102°49′501″E, 2,200 m above sea level) around Kunming, Yunnan Province, southwest China. For each species, seeds were collected from a minimum of ten individuals and mixed. The seeds of the invader were collected in one site because growth and reproduction traits are not significantly different for *E. adenophorum* plants grown from seeds collected from different populations (Zhao et al. 2009). In July 2007, the seeds were sown in a seedbed in a shadehouse with two layers of black nylon shade netting. In September 2007, when the seedlings were ~5 cm tall, similar-sized seedlings were transplanted singly into 23 dm^3 pottery pots, which were filled with forest top soil and river sand (7:3, v:v). In order to provide a natural supply of macro- and micro-nutrients, the forest top soil was collected in a location where neither *E. adenophorum* nor *E. japonicum* was found. The river sand was collected in a clean river and screened two times to remove big and fine granules in order to improve soil drainage and facilitate harvest of plant roots. Thus, the growth substrate may not cause biased results. The pH value of the substrate was 5.96, and the contents of organic matter, total N, total phosphorus, total potassium, total calcium, active N, and active phosphorus were 5.07 g kg^{-1}, 0.23 g kg^{-1}, 0.38 g kg^{-1}, 6.30 g kg^{-1}, 7.08 g kg^{-1}, 17.8 mg kg^{-1}, and 1.81 mg kg^{-1}, respectively. After 2 weeks of growth in the shadehouse (36 % irradiance), half of the seedlings of each species were moved to full sunshine (100 % irradiance). *Eupatorium adenophorum* can invade habitats with irradiance from partial shade to full sunshine (Zheng et al. 2009). It often forms dense monocultures in open sites.

The shadehouse (56.0, 4.0, and 2.7 m in length, width, and height, respectively) was built using 0.25 × 4.00 cm^2 angle irons. The relative irradiance in the shadehouse was estimated by comparing the integrated photosynthetic photon flux density in it during a clear day with that in an open site. Quantum sensors and HOBO weather station (Onset Computer Corporation, Bourne, USA) were used to measure photosynthetic photon flux density. The lower 20 cm of the shadehouse remained open to facilitate airflow and to reduce the potential effects of other environmental factors except irradiance.

In May 2008, seedlings of each species grown at each irradiance were randomly divided into four groups, 40 seedlings per group, and were fertilized with NH_4NO_3 of 0.0, 0.2, 0.4, and 0.8 g N kg^{-1} soil, respectively. NH_4NO_3 was applied three times at 10-day intervals. Total and active N contents were lower in the growth substrate used in this experiment than that used by Wang and Feng (2005). Thus, the highest N addition (0.8 g kg^{-1}) was included in this study. In addition, N was applied again at the same rates in May 2009. The seedlings grown at each irradiance were assigned to 40 rows, 8 seedlings per row (2 species × 4 N additions), and the seedlings in each row were randomly arranged. Seedlings were watered daily with drip-irrigation systems. Weeds were pulled out when necessary and no pesticides were used during the experiment.

Measurements of ecophysiological traits

In September 2009, photosynthetic response to intercellular CO_2 concentration was determined for the youngest fully expanded leaf of each sample plant (3–5 replicates for each species and treatment) using a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE). Under 1,500 μmol m^{-2} s^{-1} irradiance (>saturating photosynthetic photon flux density of each sample plant), gas exchange variables were recorded after 200 s at each of 380, 300, 260, 220, 180, 140, 110, 80, and 50 μmol mol^{-1} CO_2 in the reference chamber. Relative humidity of the air in leaf chamber was controlled at ≈50 %, and leaf temperature at 25 °C. Light-saturated photosynthetic rate (P_{max}), stomatal conductance, and intercellular CO_2 concentration presented in this study were the values measured at 380 μmol mol^{-1} CO_2 and 1,500 μmol m^{-2} s^{-1} irradiance. Light- and CO_2-saturated photosynthetic rate was detected after 500 s under 1,500 μmol m^{-2} s^{-1} irradiance and 1,500 μmol mol^{-1} CO_2. The measurements were done during 8:00–11:00, when the maximum photosynthesis can be measured. Before the measurements, each sample leaf was illuminated with saturating irradiance provided by the LED light source of the equipment to achieve full photosynthetic induction.

Three to eight fully expanded leaves were collected from the plants on which photosynthesis was measured, and oven-dried at 60 °C for 48 h after area was determined using a Li-3000C Portable Leaf Area Meter (Li-Cor, Lincoln, NE). Specific leaf area (SLA) was calculated as the ratio of leaf area to mass, which was used to transform area-based variables (stomatal conductance and P_{max}) to mass-based variables in this study. Leaf N and carbon concentrations were measured using a Vario MAX CN Element analyzer (Elementar Analysensysteme GmbH, Hanau, Germany); leaf phosphorus concentration (P_L) was measured using an inductively coupled plasma atomic emission spectrometer (IRIS Advantage-ER, Thermo Jarrell Ash Corporation, MA, USA). Leaf chlorophyll was extracted with 80 % acetone and determined using a spectrophotometer (Lichtenthaler and Wellburn 1983).

With measured values of photosynthesis, chlorophyll concentration, and N_L, the fraction of leaf N allocated to photosynthesis and N concentration in the photosynthetic apparatus were calculated after Feng et al. (2007). Photosynthetic N- and P-use efficiencies were calculated as the ratios of P_{max} to N_L and P_L, respectively.

Three to five fully expanded leaves were collected from three plants per species per treatment on which photosynthesis was measured, immediately put into a liquid N container after leaf area determination, and were then transported to laboratory for measurements of Rubisco and cell walls. The frozen leaves were powdered in liquid N, suspended in sodium phosphate buffer (pH 7.5), and were centrifuged at 15,000×g for 5 min (Eppendorf AG 5424, Hamburg, Germany). The supernatant and deposit were used to measure N in Rubisco and cell walls, respectively. Rubisco concentration was measured using enzyme-linked immunosorbent assay (Catt and Millard 1988). Anti-Rubisco (RbcL from chicken; R4404, Sigma) and HRP-conjugated goat anti-chicken serum (C1036, Sigma) were used as the primary and secondary antibodies, respectively, and A_{405} was determined with a microplate reader (Bio-Rad 550, Bio-Rad Laboratories Inc, Hercules, USA). Nitrogen in Rubisco was calculated with the conversion coefficient of 0.16 g N g^{-1} Rubisco (mean N content of proteins; Feng et al. 2009). Cell walls in the deposit were washed with strong solvents (SDS and KOH) (Onoda et al. 2004) and centrifuged, and the deposit was weighed after drying and N concentration in cell walls was measured using a Vario MAX CN Element analyzer. Fraction of leaf mass in cell walls was calculated as the ratio of cell wall mass to leaf mass. Fractions of leaf N allocated to Rubisco and cell walls were calculated as the ratios of N concentration in Rubisco and N concentration in cell walls to N_L, respectively.

Five fully expanded leaves were collected from five plants per species per treatment, and oven-dried at 60 °C for 48 h. The heat of combustion (HC) of the leaves was determined using a Sundy Microbomb Calorimeter (SDCM-IIIa, Changsha Sundy Industrial Co., Ltd., Changsha, China). The calorimeter was calibrated with a benzoic acid standard of known caloric value before measurements. Powdered leaves were burned in a muffle furnace at 550 °C for 4 h to determine ash concentration (Ash). Leaf CC (g glucose g^{-1}) was calculated as $CC = ((0.06968 \times HC - 0.065) \times (1 - Ash) + 7.5 \times (k \times N_L/14.0067)) \times (1/E_G)$, where k is the oxidation state of the N absorbed and E_G is the growth efficiency (0.89; Williams et al. 1987). In this study, $k = +5$ as nitrate is the principal N source for high

plants (Taiz and Zeiger 1991). PEUE was calculated as the ratio of P_{max} to CC.

After the measurements mentioned above, ten individuals (including roots) per species per treatment were harvested, oven-dried at 60 °C for 48 h, and weighed.

Leaf phenology

From March 2008 to March 2009, leaf phenology was observed weekly for *E. adenophorum* and its native congener grown in 0 and 0.4 g N additions kg^{-1} soil under 36 % irradiance. Attention was paid to the patterns of leaf emergence and shedding. To measure leaf lifespan, more than 270 newly emerged leaves (5–8 leaves per plant) were labeled in summer, and were observed weekly until death (90 % of leaf area became brown). Total leaf area was measured monthly on four individuals per species per each of the two treatments in situ (but not in April, June, and November) using a Li-3000C Portable Leaf Area Meter. To evaluate the physiological function of the leaves persistent in winter, P_{max} was measured on four individuals of the invader in the months when native *E. japonicum* had no living leaves. To understand how biomass of the invader was affected by its ability to capture resources not available to native *E. japonicum*, eight individuals (including roots) from each of the two N additions were harvested for the invader on October 22, 2008 (*E. japonicum* began to senesce) and March 15, 2009 (*E. japonicum* began to grow leaves), respectively, oven-dried at 60 °C for 48 h, and weighed.

Statistical analyses

Effects of species, irradiance, N addition, and their interactions on the ecophysiological variables measured in this study were tested using three-way ANOVAs, with species ($n = 2$), irradiances ($n = 2$), and N additions ($n = 4$) as fixed factors. The differences in the variables among N additions for the same species grown at the same irradiance, the differences in total leaf area measured in each month among N additions and species, and the differences in total biomass measured in October 2008 and March 2009 among N additions and months were tested using one-way ANOVAs. Sequential Bonferroni correction for multiple comparisons was not conducted to reduce experiment-wide type I error to 0.05; it may increase the probability of type II error (Moran 2003). Duncan's new multiple range test was used in multiple comparisons and all P values were presented. The differences in the variables between irradiances for the same species grown at the same N addition, the differences in the variables between the invasive and native species grown under the same irradiance and N addition, and the differences in P_{max} measured for *E. adenophorum* when *E. japonicum* was leafless between N additions were tested using independent samples t test. One-way ANCOVAs were used to determine the differences between the invasive and native species in the correlation between each pair of the variables shown in Table 2; species was used as a fixed factor, and dependent and independent variables in each equation were used as dependent variable and covariate, respectively. If the difference was significant, we then tested for significance of linear Pearson correlations (two-tailed) for invasive and native species separately; otherwise, we pooled data from the two species to test for the significance of the correlations. Homogeneity of variances was tested before analyses, and data were transformed to meet the assumption of ANOVA if homogeneity of variances was not equality. All the analyses were carried out using SPSS 13.0 (SPSS Inc., Chicago, IL).

Results

According to the results of three-way ANOVAs, all 17 traits measured in September 2009 were significantly influenced by species, 14 traits by irradiance (i.e. plastic to irradiance), and 10 traits by N (i.e. plastic to N; Table S1). The effects of irradiance were much higher than those of N. Below we compared the differences between the invasive and native species.

Ecophysiological traits

Leaf N concentration was not significantly different between invasive *E. adenophorum* and native *E. japonicum* under all eight treatment combinations of two irradiances and four N additions (all $P > 0.05$) except 0.0 g N addition kg^{-1} soil of 36 % irradiance, in which the invader demonstrated lower N_L ($P < 0.05$; Table 1). However, the invader had a higher fraction of leaf N allocated to photosynthesis than *E. japonicum* in all treatments ($P < 0.05$), while the fraction of leaf N allocated to cell walls was not

significantly different between the two species ($P > 0.05$; Table 1). The fraction of leaf N allocated to Rubisco was also higher for the invader than for *E. japonicum*, although the differences were not significant in some treatments. The invader showed a higher N concentration in the photosynthetic apparatus than *E. japonicum* in all treatments ($P < 0.05$; Table 1).

Compared with *E. japonicum*, invasive *E. adenophorum* had significantly higher P_{max}, stomatal conductance (with three exceptions), PNUE, PPUE (with one exception), and PEUE in all treatments (all $P < 0.05$; Table 1). The invader had higher CC than *E. japonicum* at 36 % irradiance ($P < 0.05$) but not at 100 % irradiance (except in 0.8 g N addition kg^{-1} soil; $P = 0.0058$).

Invasive *E. adenophorum* had significantly higher SLA in most treatments (with two exceptions; Table 1). The fraction of leaf mass in cell walls was lower for the invader in all treatments (with one exception). At 100 % irradiance, the invader had lower P_L (with one exception) and higher N to P ratio ($P < 0.05$). These trends remained at 36 % irradiance, but the differences were not significant except for N to P ratio in 0.8 g N addition kg^{-1} soil ($P = 0.0002$; Table 1).

Similarly, higher P_{max}, PNUE, PEUE, stomatal conductance, CC, and SLA, and similar N_L were also measured for *E. adenophorum* compared with *E. japonicum* in September, 2008 (Table S2).

Light-saturated photosynthetic rate increased significantly with increasing the fraction of leaf N allocated to photosynthesis, N concentration in the photosynthetic apparatus, and stomatal conductance (all $P < 0.05$; Table 2). Photosynthetic N-use efficiency, PPUE, and PEUE increased significantly with increasing P_{max}. With increasing P_L, PPUE decreased, and with increasing N to P ratio, PPUE increased significantly at 100 % irradiance but not at 36 % irradiance.

Leaf phenology

Native *E. japonicum* initiated leaf growth in early April 2008, shed almost all leaves in early November, and began to bud in late March 2009. It had no functional leaves in the winter (roughly 5 months). The invader maintained green throughout the entire year, although it shed many leaves in March and April (during seed maturity). In the growing season of *E. japonicum* (April–October), total leaf area was higher for the invader than for its native congener ($P < 0.05$; Fig. 1). Total leaf area of the invader did not decrease significantly in the months in which *E. japonicum* was leafless (November–March), and the leaves persistent and green in winter had relatively high P_{max} (Fig. 2). Leaf lifespan was significantly longer ($P < 0.001$) for the invader (118.24 ± 2.926, $n = 150$) than for *E. japonicum* (90.03 ± 4.033, $n = 117$). Nitrogen addition did not significantly influence leaf lifespan.

Total biomass of the invader was significantly higher on March 15, 2009 (when *E. japonicum* began to grow) than on October 22, 2008 (when *E. japonicum* began to senesce; Fig. 3). The biomass accumulated during the period when *E. japonicum* did not grow accounted for 42.7 and 41.8 % of total biomass of the invader in 0.0 and 0.4 g N additions kg^{-1} soil, respectively. The invader was much higher in total biomass than *E. japonicum* at the end of the study (September 2009; Table 1).

Discussion

Many studies attribute invasion success of alien species to their growth advantages over co-occurring natives (Zheng et al. 2009; Dawson et al. 2011; Lamarque et al. 2011). However, few studies have explored the potential mechanisms underlying the growth advantages of invasive plants. Here we found that both physiological advantages and prolonged growth season contributed to the growth advantage of *E. adenophorum* over its native congener under all eight treatment combinations of two irradiances and four N additions in a two-year shadehouse experiment.

Physiological advantages of the invader

Invasive *E. adenophorum* achieved significantly higher P_{max} with similar or even lower N_L compared with its native congener under all eight treatment combinations of two irradiances and four N additions, inconsistent with the positive correlation between photosynthetic rate and N_L (Reich et al. 1997). The higher P_{max} of the invader was associated with its higher N concentration in the photosynthetic apparatus (Table 2), which was caused by its higher N allocation to photosynthesis including Rubisco. The

Table 1 Differences in traits measured in September 2009 between invasive *Eupatorium adenophorum* and native *E. japonicum* grown in different treatments

Irradiance		100 %				36 %			
N addition (g *N* kg^{-1} soil)		0.0	0.2	0.4	0.8	0.0	0.2	0.4	0.8
Growth									
Biomass	*E. adenophorum*	50.36 ± 5.818*	35.48 ± 4.140*	48.19 ± 6.983	37.03 ± 2.169*	150.7 ± 19.72*+	178.1 ± 17.66*+	241.4 ± 41.69*+	201.4 ± 19.40*+
	E. japonicum	21.64 ± 4.214	18.59 ± 1.622	35.47 ± 11.43	23.38 ± 4.418	13.89 ± 1.534	44.72 ± 7.876	25.45 ± 3.105	28.34 ± 2.355
Nitrogen allocation									
N_L	*E. adenophorum*	17.70 ± 0.317a	16.31 ± 0.109ab	17.25 ± 0.864ab	16.08 ± 0.158b	18.49 ± 0.501c	19.73 ± 0.165b+	21.23 ± 0.426a+	21.46 ± 0.358a+
	E. japonicum	19.41 ± 1.135a	17.10 ± 0.783b	17.92 ± 0.173ab	17.09 ± 0.522b	22.97 ± 0.504a*+	22.80 ± 1.545a+	22.11 ± 0.771a+	21.35 ± 0.710a+
$N_{Photosynth}$	*E. adenophorum*	12.91 ± 0.690*	12.87 ± 0.619*	13.25 ± 0.221*	13.64 ± 0.663*	16.07 ± 0.596b*+	17.41 ± 0.352b*+	18.90 ± 0.286a*+	17.50 ± 0.536b*+
	E. japonicum	7.33 ± 0.609b	7.54 ± 1.152b	9.27 ± 0.452ab	11.59 ± 0.400[a]	11.29 ± 0.815c +	12.64 ± 0.172bc+	14.89 ± 0.638a+	14.25 ± 0.365ab+
$N_{photosynth}/N_L$	*E. adenophorum*	0.715 ± 0.031b*	0.792 ± 0.039ab*	0.792 ± 0.050ab*	0.842 ± 0.032a*	0.857 ± 0.025*	0.882 ± 0.011*+	0.893 ± 0.025*	0.834 ± 0.011*
	E. japonicum	0.378 ± 0.030c	0.436 ± 0.054bc	0.533 ± 0.033b	0.679 ± 0.028[a]	0.474 ± 0.027c	0.554 ± 0.023bc	0.625 ± 0.036ab	0.668 ± 0.019a
$N_{Rubisco}/N_L$	*E. adenophorum*	0.166 ± 0.014b*	No data	0.167 ± 0.022b	0.299 ± 0.038a*	0.199 ± 0.020*	No data	0.198 ± 0.031	0.257 ± 0.034
	E. japonicum	0.089 ± 0.007b	No data	0.102 ± 0.015b	0.147 ± 0.002a	0.136 ± 0.008+	No data	0.162 ± 0.022	0.187 ± 0.026
N_{CW}/N_L	*E. adenophorum*	0.146 ± 0.016	No data	0.170 ± 0.012+	0.170 ± 0.016+	0.114 ± 0.009	No data	0.111 ± 0.008	0.110 ± 0.003
	E. japonicum	0.127 ± 0.011+	No data	0.147 ± 0.022	0.167 ± 0.006+	0.091 ± 0.006	No data	0.101 ± 0.010	0.108 ± 0.005
Photosynthesis and photosynthetic resource-use efficiency									
P_{max}	*E. adenophorum*	0.181 ± 0.017b*	0.189 ± 0.013ab*	0.192 ± 0.008ab*	0.222 ± 0.009a*	0.272 ± 0.013*+	0.288 ± 0.015*+	0.291 ± 0.004*+	0.293 ± 0.008*+
	E. japonicum	0.114 ± 0.008b	0.125 ± 0.009b	0.128 ± 0.008b	0.181 ± 0.004a	0.175 ± 0.010b+	0.170 ± 0.009b+	0.215 ± 0.005a+	0.200 ± 0.012ab
G_s	*E. adenophorum*	2.489 ± 0.336b	4.294 ± 0.855a	3.446 ± 0.412ab*	4.223 ± 0.362a*	3.798 ± 0.502b	5.627 ± 0.683a*	6.240 ± 0.231a*+	5.639 ± 0.255a*+
	E. japonicum	2.057 ± 0.274b	2.258 ± 0.277b	2.148 ± 0.250b	3.094 ± 0.120a	2.766 ± 0.173+	3.478 ± 0.124+	3.803 ± 0.316+	3.464 ± 0.632
PNUE	*E. adenophorum*	9.53 ± 0.807b*	10.65 ± 0.687b*	11.54 ± 1.040ab*	13.70 ± 0.511a*	14.26 ± 0.946*+	14.11 ± 1.011*+	13.75 ± 0.441*	13.53 ± 0.314*
	E. japonicum	6.05 ± 0.516b	7.32 ± 0.613b	7.17 ± 0.457b	10.88 ± 0.293a+	7.64 ± 0.386b+	7.90 ± 0.398ab	9.31 ± 0.267a+	9.06 ± 0.537ab
PEUE	*E. adenophorum*	0.131 ± 0.008*	0.130 ± 0.010*	0.136 ± 0.007*	0.153 ± 0.006*	0.183 ± 0.014*+	0.208 ± 0.013*+	0.197 ± 0.005*+	0.193 ± 0.006*+
	E. japonicum.	0.082 ± 0.005b	0.094 ± 0.008b	0.092 ± 0.004b	0.136 ± 0.003a	0.131 ± 0.007b+	0.131 ± 0.007b+	0.156 ± 0.005a+	0.141 ± 0.008ab
PPUE	*E. adenophorum*	122.30 ± 16.27b	120.60 ± 9.933b*	138.70 ± 4.985b*	172.30 ± 7.333a*	174.50 ± 8.485*+	174.90 ± 10.92*+	187.70 ± 2.835*+	171.90 ± 9.955*
	E. japonicum.	71.20 ± 7.000ab	59.28 ± 3.072b	54.55 ± 7.181b	87.85 ± 7.154a	95.38 ± 7.845	106.10 ± 5.999+	108.90 ± 9.630+	99.64 ± 4.845
Leaf construction cost and others									
CC	*E. adenophorum*	1.426 ± 0.010ab	1.396 ± 0.008c	1.411 ± 0.008bc	1.444 ± 0.007a*	1.440 ± 0.010b*	1.424 ± 0.010b*	1.466 ± 0.025ab*	1.505 ± 0.013a*+
	E. japonicum	1.385 ± 0.016ab+	1.377 ± 0.015ab	1.414 ± 0.016a+	1.348 ± 0.023b	1.322 ± 0.008	1.324 ± 0.023	1.334 ± 0.011	1.351 ± 0.008
HC	*E. adenophorum*	19.36 ± 0.113	19.24 ± 0.131	19.15 ± 0.080	19.40 ± 0.076	19.49 ± 0.120b*	19.31 ± 0.120b	19.69 ± 0.224ab*+	20.02 ± 0.133a*+
	E. japonicum	19.47 ± 0.186ab+	19.57 ± 0.131ab+	19.88 ± 0.192a*+	19.12 ± 0.242b	18.84 ± 0.157	18.81 ± 0.253	18.85 ± 0.113	19.07 ± 0.086
P_L	*E. adenophorum*	1.558 ± 0.073a	1.523 ± 0.100a	1.380 ± 0.033ab	1.288 ± 0.004b	1.634 ± 0.144	1.770 ± 0.200	1.576 ± 0.037+	1.722 ± 0.094+
	E. japonicum	1.537 ± 0.012b	2.030 ± 0.171a*	2.117 ± 0.147a*	2.137 ± 0.147a*	1.973 ± 0.139	1.722 ± 0.078	1.894 ± 0.166	1.970 ± 0.054
N to P ratio	*E. adenophorum*	10.91 ± 0.495b*	11.24 ± 0.068b*	12.70 ± 0.530a*	11.90 ± 0.207ab*	12.26 ± 0.172+	11.71 ± 1.704	12.15 ± 0.214	13.95 ± 0.232*+
	E. japonicum	8.55 ± 0.049	7.24 ± 0.944	6.53 ± 0.485	7.11 ± 0.596	10.97 ± 0.746	10.17 ± 0.394+	11.05 ± 0.662+	9.26 ± 0.668
SLA	*E. adenophorum*	160.3 ± 4.837a*	154.0 ± 1.039ab*	155.0 ± 3.176ab*	147.1 ± 3.795b*	212.0 ± 6.417b+	223.0 ± 2.212a*+	216.6 ± 1.915ab*+	195.0 ± 1.508c+
	E. japonicum	117.2 ± 0.447b	124.5 ± 3.134a	117.0 ± 2.151b	122.3 ± 0.903ab+	213.1 ± 2.865a+	203.7 ± 9.481ab+	188.9 ± 4.612b+	191.5 ± 10.00b+

Table 1 continued

		Irradiance	100 %				36 %			
		N addition (g *N* kg^{-1} soil)	0.0	0.2	0.4	0.8	0.0	0.2	0.4	0.8
M_{CW}/M_L	*E. adenophorum*		0.270 ± 0.010	No data	0.279 ± 0.014	0.264 ± 0.021+	0.235 ± 0.011	No data	0.218 ± 0.019	0.187 ± 0.015
	E. japonicum		0.341 ± 0.007*+	No data	0.353 ± 0.007*	0.361 ± 0.017*	0.290 ± 0.056	No data	0.338 ± 0.016*	0.333 ± 0.005*

Mean ± SE (n = 3–5). Different letters indicate significant differences among N additions for the same species grown at the same irradiance according to one-way ANOVA ($P < 0.05$)

* Indicates significant difference between species grown in the same irradiance and N addition according to independent samples t test ($P < 0.05$)

+ Depicts significant difference between irradiances for the same species grown in the same N addition according to independent samples t test ($P < 0.05$)

CC (g glucose g−1) leaf construction cost; G_s (mol g^{-1} s^{-1}) stomatal conductance; *HC* (kJ g^{-1}) heat of combustion of leaf; M_{CW}/M_L (g g^{-1}) fraction of leaf mass in cell walls; *N:P ratio* (g g^{-1}) ratio of leaf nitrogen to phosphorus; N_{CW}/N_L (g g^{-1}) fraction of leaf nitrogen in cell walls; N_L (mg g^{-1}) leaf nitrogen concentration; $N_{photosynth}$ (mg g^{-1}) nitrogen concentration in the photosynthetic apparatus; $N_{photosynth}/N_L$ (g g^{-1}) fraction of leaf nitrogen allocated to photosynthesis; $N_{Rubisco}/N_L$ (g g^{-1}) fraction of leaf nitrogen allocated to Rubisco; P_L (mg g^{-1}) leaf phosphorus concentration; P_{max} (μmol g^{-1} s^{-1}) light-saturated photosynthetic rate; PEUE (μmol g^{-1} s^{-1}) photosynthetic energy-use efficiency; *PNUE* (μmol g^{-1} s^{-1}) photosynthetic nitrogen-use efficiency; *PPUE* (μmol g^{-1} s^{-1}) photosynthetic phosphorus-use efficiency; *SLA* (cm^2 g^{-1}) specific leaf area

higher P_{max} of the invader contributed to higher daily net CO_2 assimilation, which combined with higher total leaf area led to higher total biomass.

The higher N allocation to photosynthesis may be associated with the fact that the invader suffers less herbivory than its native congener (Fig. S1; Zheng et al. 2012). In response to enemy release, *E. adenophorum* appears to have evolved increased N allocation to photosynthesis and decreased allocation to defense (Feng et al. 2009). However, the tradeoffs for N allocation to photosynthesis versus cell walls may not explain the invader's higher fraction of leaf N in photosynthesis because the fraction of leaf N in cell walls was not significantly different between the invader and its native congener. Interspecific differences in N allocated to N-based defensive compounds such as alkaloids and cyanogenic glycosides may be likely to explain the invader's higher fraction of leaf N allocated to photosynthesis. In some eucalypts, cyanogenic glycosides account for more than 10 % of leaf N and accumulation of these chemicals reduces net assimilation rates (Goodger et al. 2006).

A positive correlation between P_{max} and SLA has been documented in many studies (Reich et al. 1997; Feng et al. 2007). Thus, the higher SLA of *E. adenophorum* relative to native *E. japonicum* may also contribute to its higher P_{max}. A negative correlation between SLA and the fraction of leaf mass in cell walls ($P < 0.001$; data not shown) indicated that the higher SLA of the invader may derive from a lower fraction of leaf mass in cell walls. These two traits are associated with leaf density and toughness, and therefore are important measures of plant defenses (Wright and Cannon 2001; Kurokawa and Nakashizuka 2008).

Unlike the higher PNUE in *E. adenophorum* compared with its native congener, which was due to its higher P_{max}, both the higher P_{max} and the lower P_L contributed to its higher PPUE (Table 2). The negative correlation between PPUE and P_L indicated that P_L is higher than the optimum concentration, below which a positive correlation between PPUE and P_L is expected. The positive correlation between PPUE and N to P ratio indicated that N is the limiting factor for photosynthesis, providing further evidence that the invader benefited from increasing N allocation to photosynthesis. In this study, P_L was indeed higher and N to P ratio is lower than those of 753 native species in China on average (1.21 mg g^{-1} and 14.4,

Table 2 Correlations between each pair of the traits

Irradiance Intercept and slope	36 %				100 %			
	a	b	*r*	*P*	a	b	*r*	*P*
$P_{max} = a + b \times N_{photosynth}$								
Invasive species	0.065	0.013	0.653	0.003				
Native species	0.076	0.009	0.677	0.016				
Invasive and native species					0.010	0.014	0.896	<0.001
$P_{max} = a + b \times N_{photosynth}/N_L$								
Invasive and native species	0.005	0.320	0.895	0.009	0.029	0.212	0.890	<0.001
$P_{max} = a + b \times G_s$								
Invasive species	0.227	0.011	0.599	0.005	0.137	0.016	0.748	<0.001
Native species	0.116	0.022	0.604	0.010	0.053	0.036	0.828	<0.001
$PNUE = a + b \times P_{max}$								
Invasive and native species	−1.912	55.78	0.959	<0.001	−0.550	61.12	0.904	<0.001
$PEUE = a + b \times P_{max}$								
Invasive species	−0.011	0.718	0.779	<0.001				
Native species	0.013	0.682	0.988	<0.001				
Invasive and native species					0.007	0.673	0.992	<0.001
$PPUE = a + b \times P_{max}$								
Invasive species	164.8	42.21	0.044	0.862	−39.23	917.6	0.916	<0.001
Native species	37.28	361.1	0.501	0.081	17.23	375.1	0.798	0.002
$PPUE = a + b \times P_L$								
Invasive species	273.3	−58.75	0.732	<0.001	349.4	−147.0	0.792	<0.001
Native species	167.7	−34.36	0.717	0.006	88.87	−10.88	0.227	0.457
PPUE = a + b × N to P ratio								
Invasive species	199.1	−1.558	0.152	0.561				
Native species	104.9	−0.183	0.018	0.953				
Invasive and native species					−41.67	15.31	0.864	0.006

Linear Pearson correlations (two-tailed) for invasive and native species were given separately if the difference in the correlation between species was significant according to ANCOVA; otherwise, the correlation for the pooled data from both species was given

G_s (mol g^{-1} s^{-1}) stomatal conductance; $N_{photosynth}$ (mg g^{-1}) nitrogen concentration in the photosynthetic apparatus; $N_{photosynth}/N_L$ (g g^{-1}) fraction of leaf nitrogen allocated to photosynthesis; P_L (mg g^{-1}) leaf phosphorus concentration; P_{max} (μmol g^{-1} s^{-1}) light-saturated photosynthetic rate; *PEUE* (μmol g^{-1} s^{-1}) photosynthetic energy-use efficiency; *PNUE* (μmol g^{-1} s^{-1}) photosynthetic nitrogen-use efficiency; *PPUE* (μmol g^{-1} s^{-1}) photosynthetic phosphorus-use efficiency

respectively; Han et al. 2005). Similarly, Kurokawa et al. (2010) also found positive correlation between invasiveness and leaf N to P ratio.

Contrary to our prediction, invasive *E. adenophorum* had higher CC than native *E. japonicum*, especially at low irradiance, which was associated with its higher HC and carbon concentration (Table 1). Higher CC was also documented for invasive species of the Poaceae family relative to natives (Baruch and Goldstein 1999), while most related studies found lower CC for invasive species (Nagel and Griffin 2001; Daehler 2003; Song et al. 2009; Osunkoya et al. 2010). However, the higher CC of the invader did not decrease its benefit–cost ratio; instead it showed higher PEUE (Table 1). Leaves can maximize lifetime net carbon gain by increasing lifespan and/or PEUE. The results indicated that *E. adenophorum* was located at the fast-return end of leaf economics spectrum, showing a quicker-return energy-use strategy despite higher CC. This energy-use strategy of the invader was apparently associated with its higher P_{max}. Higher PEUE was also found for other invasive species compared with co-occurring natives (Song et al. 2009; Funk and Vitousek 2007; Feng et al. 2011).

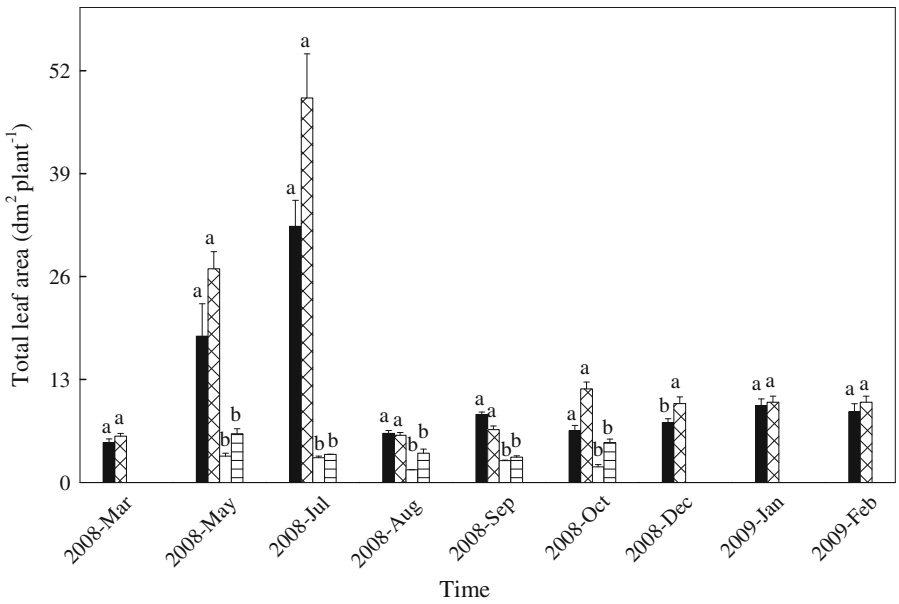

Fig. 1 Total leaf area for *Eupatorium adenophorum* (*closed bar* 0.0 g N addition kg^{-1} soil; *hatched bar* 0.4 g N addition kg^{-1} soil) and *E. japonicum* (*open bar* 0.0 g N addition kg^{-1} soil; *striped bar* 0.4 g N addition kg^{-1} soil) grown at 36 % irradiance. Mean ± SE ($n = 4$). *Different letters* indicate significant differences among species and nitrogen additions in each month ($P < 0.05$). Effects of species (S), nitrogen (N), month (M), and their interactions were analyzed using three-way ANOVA (S, $F = 377.62$, $P < 0.001$; N, $F = 13.09$, $P = 0.001$; M, $F = 62.54$, $P < 0.001$; S × N, $F = 7.18$, $P = 0.009$; S × M, $F = 81.39$, $P < 0.001$; N × M, $F = 3.72$, $P = 0.001$; S × N × M, $F = 5.63$, $P < 0.001$)

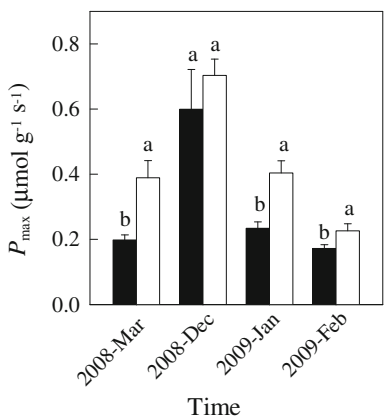

Fig. 2 Light-saturated photosynthetic rate (P_{max}) for *Eupatorium adenophorum* grown in 0.0 (*closed bar*) and 0.4 g N additions kg^{-1} soil (*open bar*) under 36 % irradiance. Mean ± SE ($n = 4$). *Different letters* indicate significant differences between nitrogen additions in the same month ($P < 0.05$)

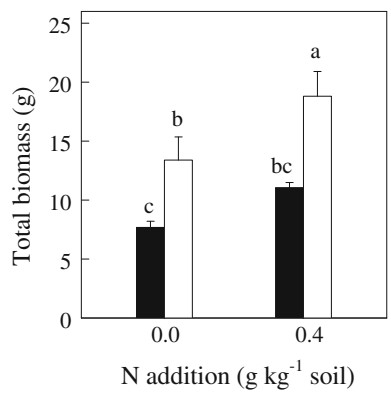

Fig. 3 Total biomass for *Eupatorium adenophorum* grown in 0.0 and 0.4 g N additions kg^{-1} soil under 36 % irradiance. Mean ± SE ($n = 8$). *Closed* and *open bars* indicate data measured on October 22, 2008 (when *E. japonicum* began to senesce) and Mar 15, 2009 (when *E. japonicum* began to grow), respectively. *Different letters* indicate significant differences among nitrogen additions and months ($P < 0.05$)

Prolonged growth season of the invader

In winter, when native *E. japonicum* was leafless, *E. adenophorum* maintained a large area of living leaves, which showed relatively high P_{max} and achieved high actual daily carbon gain (data not shown). The amount of the carbon accumulated in winter contributed greatly to total biomass for the invader (Fig. 3). Prolonged growth season has been proposed to explain the competitive advantages of other invasive species

over co-occurring natives (Xu et al. 2007; Fridley 2012). In the temporal empty niche, invasive species can capture a significant proportion of their annual carbon gain. This trend was aggrandized by the overwintering leaves of *E. adenophorum,* which accumulated more than 40 % total biomass in this period.

Schlesinger and Chabot (1977) hypothesized that leaves with different lifespan may gain similar amount of carbon over entire lifetime, which is consistent with the fact that increasing leaf lifespan can maximize lifetime net carbon gain per unit leaf mass but may decrease mass-based P_{max} (Reich et al. 1997). However, this was not the case for *E. adenophorum*. The invader had both longer leaf lifespan and higher P_{max} than its native congener, resulting in much higher leaf carbon gain over lifetime. The invader had longer leaf lifespan and higher SLA than its native congener, inconsistent with the general negative correlation between SLA and leaf lifespan for plants from tropics to tundra (Reich et al. 1997). Insects and pathogens are likely to contribute to the shorter leaf lifespan of *E. japonicum* (Fig. S1).

In conclusion, compared with native *E. japonicum* invasive *E. adenophorum* had higher light-saturated photosynthetic rate, PEUE, total leaf area, and longer leaf lifespan, contributing to carbon and energy gain at both leaf and whole-plant levels, biomass accumulation, and therefore invasiveness. Higher nitrogen allocation to photosynthesis, SLA, and stomatal conductance of the invader contributed to its higher photosynthesis, which in turn caused higher photosynthetic nitrogen-, phosphorus- and energy-use efficiencies. In winter when the native congener was leafless (November–March), the invader maintained a large area of leaves with active photosynthesis, contributing to its growth advantage not only directly by accumulating extra biomass in winter but also indirectly by shading its native congener in early spring. The invader retained advantages over its native congener under all eight treatment combinations of two irradiances and four nitrogen additions, indicating that decreasing irradiance and soil nitrogen availability may not mitigate its invasion. Our study showed the potential mechanisms underlying growth advantage of invasive plant species.

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